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Macroevolutionary evidence suggests trait-dependent coevolution between behaviour and life-history

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AGV and BR conceived the study. The planning of the study was conducted by SE, PR, WS, AGV and BR. The first draft of the manuscript was written by SE, all authors contributed to the final version. The data collection was performed by SE with the help of WS. The data analysis was conducted by SE, SM, WvdB and BR.

Keywords: killifish, life-history trade-offs, pace-of-life syndrome (POLS) hypothesis, risk-taking behaviour, standard metabolic rate (SMR)

ABSTRACT

Species with fast life-histories typically prioritize current over future reproductive events, compared to species with slow life-histories. These species therefore require greater energetic input into reproduction, and also likely have less time to realize their reproductive potential. Hence, behaviours that increase access to both resources and mating opportunities, at a cost of increased mortality risk, could coevolve with the pace of life-history. However, whether this prediction holds across species, remains untested under standardized conditions. Here, we test how risky behaviours, which facilitate access to resources and mating opportunities (i.e. activity, boldness and aggression), along with metabolic rate, coevolve with the pace of life-history across 20 species of killifish that present remarkable divergences in the pace of life-history. We found a positive association between the pace of life-history and aggression, but interestingly not with other behavioural traits or metabolic rate. Aggression is linked to interference competition, and in killifishes is often employed to secure mates, while activity and boldness are more relevant for exploiting energetic resources. Our results suggest that the trade-off between current and future reproduction plays a more prominent role in shaping mating behaviour, while behaviours related to energy acquisition may be influenced by ecological factors.

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INTRODUCTION

Potentially risky behaviours, such as activity, boldness and aggression, can provide increased access to resources and mating opportunities, while simultaneously increasing the chances of injury and predation (Smith and Blumstein 2008). We therefore could expect animals to behave optimally, by plastically adjusting their expression of risk-taking behaviours, according to the current mortality risk (Coleman and Wilson 1998; Wilson 1998; Dall et al. 2004; Sih et al. 2004b; Réale et al. 2007; Snell-Rood 2013). This prediction contrasts with the observation that individuals often display consistent differences in risk-taking behaviours, across time and context, suggesting that differences in behaviour do not arise solely due to plasticity (e.g. personalities, Wilson et al. 1994; Boissy 1995; Gosling and John 1999). Moreover, behavioural traits associated with risk-taking frequently cluster along a broader behavioural axis from proactive to reactive behavioural types (Koolhaas et al. 1999; Groothuis and Carere 2005; Sih and Bell 2008), implying a common mechanism (see Wolf et al. 2007). Importantly, consistency in the expression of risk-taking behaviour occurs at different evolutionary levels, e.g. among individuals (Bell et al. 2009), populations (Foster 1999; Harris et al. 2010), and species (Mettke-Hofmann et al. 2004). However, to date most theoretical and empirical work has been conducted at an among-individual scale, meaning that our understanding of the evolution of these behaviours is less clear at macro-evolutionary scales (Sih et al. 2004a).

Risk-taking is inherently linked to both resource acquisition and mortality, implying a clear link between these behaviours and life-history, as well as the physiological correlates of life-histories, at different evolutionary scales (Biro and Stamps 2008; Careau et al. 2009; Réale et al. 2010; Careau and Garland 2012; Dammhahn et al. 2018; Sol et al. 2018). At the individual (phenotypic) level, empirical studies have generally found relatively weak associations

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between risk-taking behaviours and life-history (Royauté et al. 2018). In contrast, Careau et al. (2009) found that among rodent species, exploration was positively associated with age at maturity. Species-level comparative studies may differ from individual-level studies for several reasons, which may both enhance, or dilute a putative biological signal. For example, comparative studies across species may be more successful in detecting the trade-offs predicted by theory, as at the individual level, differential patterns of resource acquisition can mask trade-offs when comparing among individuals of a given population (van Noordwijk and de Jong 1986; Stearns 1989; Robinson and Beckerman 2013). On the other hand, variation in selection pressures due to ecological differences is likely to be much larger across, rather than within, evolutionarily independent units such as species and populations (Leinonen et al. 2008), which modulate evolutionary trade-offs. For example, if predation is considered to drive a positive covariation between life-history and risk-taking behaviour, yet predation differs among species**,** a species with a low predation risk will have a very different functional link between reproduction and mortality, compared to a species that is adapted to high predation risk. Hence, a species exposed to high levels of predation could be selected for both predator avoidance and a fast life-history.

Across species, life-history traits often covary along a continuum from fast to slow (Partridge and Harvey 1988; Read and Harvey 1989; Promislow and Harvey 1990; Ricklefs 2000), with two non-mutually exclusive mechanisms, potentially driving the association between behaviour and life-history . First, species with different life-histories will differ in their relative energetic demands, where species with fast life-histories are characterized by high productivity, in terms of high investment into growth and reproduction, and will therefore need to acquire greater energetic resources (Hou et al. 2008). In general, fast-living species

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need to grow fast in order to reach a species-specific body size to start reproducing as quickly as possible. Moreover, fast rates of growth and reproduction are also thought to incur fitness advantages, even if they simultaneously incur costs to other fitness components, such as long-term survival (Kirkwood 1977; Dmitriew 2011). Several behavioural traits are predicted to facilitate greater access to resources, but also increase mortality risk (Stamps 2007; Biro and Stamps 2008). For example, there is a trade-off between predation risk and foraging effort, which has been identified as a major constraint on growth rates in many taxa (Dmitriew 2011). We could therefore expect to observe differences in the expression of risk-taking behaviours between species with fast and slow life-histories. For instance, in fast-living species the benefits of taking risks, in order to secure access to resources, likely outweigh the costs of increased exposure to predators in the longer-term, whereas slow-living species have lower energetic demands and unnecessary risks may jeopardize future fitness potential.

The second potential mechanism is aligned with life-history theory, which predicts that species vary in the degree to which they emphasise current versus future reproduction, where the traits that benefit one strategy over the other, likely coevolve along this continuum (Williams 1966; Stearns 1976; Roff 1992). In support of this prediction, there is a substantial body of comparative evidence that demonstrates that species investing heavily into current reproductive events, suffer costs in regard to increased mortality rates (Gunderson and Dygert 1988; Promislow and Harvey 1990; Crespi and Teo 2002). Therefore, we would expect any traits that increase current mating success to be favoured in species that prioritize current reproduction, as any potential long-term costs are unlikely to be realized (Kirkwood 1977). For example, Andersson (1994) suggested that costly sexual traits should evolve more extreme values in species that favour current over future reproduction. Similar predictions should also be applicable to traits that are not primarily associated with energetic processes (e.g. growth rate and reproductive rate) if they increase the chances of immediate mating

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success. Likewise, the expression of risk-taking behaviours could be favoured in species that prioritize current reproduction, if such behaviours facilitate immediate mating success. Furthermore, any costs incurred by risk-taking behaviours are unlikely to be realized, as at any time point, these species will have already completed a larger fraction of their reproductive output, compared to species that prioritize future reproduction (as per the Pace of Life syndrome (POLS) hypothesis: Réale et al. 2010; Dammhahn et al. 2018).

In this study, we test the predicted coevolution between life-history, metabolism and risk-taking behaviour in a macroevolutionary comparative setting, using a common-garden experiment. Specifically, we measured behaviour and metabolic rate across 20 species of killifish. Within killifishes, several species have independently evolved to survive in ephemeral habitats, so called 'annual' killifish, with eggs that are capable of surviving habitat desiccation, by remaining dormant until the next wet season (Furness et al. 2015; Furness 2016). Across taxa, time-limited environments select for fast life-histories (e.g. Conover 1990; Rogell et al. 2009) and the prioritization of current reproduction. Likewise, killifishes living in ephemeral habitats, as opposed to 'non-annual' slow-living killifish species who occupy more stable habitats, exhibit typical characteristics of organisms with highly productive life-histories, where single egg clutches are deposited at different frequencies, depending on species (Eckerström-Liedholm et al. 2017). In a parallel study on 30 species of these killifish we show that these key life-history traits exhibit correlated evolution across three different life-history stages (juvenile - growth, young adults - time to maturity, and adults – reproduction) typical of a fast-slow axis of the pace of life-history, where annual species in general were found on the fast end, and non-annuals on the slow end of the spectrum (Sowersby et al. preprint). While this variation in life-history traits evolves in response to differences in the seasonality of habitats, desiccation is not the sole cause of mortality in annual killifishes, as mortality occurs continuously even prior to habitat

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desiccation (Vrtílek et al. 2018). This indicates the relevance of additional ecological factors, beyond seasonality (i.e. habitat desiccation), in driving extrinsic mortality.

We focused on behavioural traits (activity, boldness and aggression) that represent variation in the level of risk-taking, as they can both increase access to resources or mating opportunities, while also increasing the risks of injury or mortality. An important assumption underlying our test is that these behavioural traits facilitate increased access to resources or mating opportunities, and simultaneously increase the risk of injury or mortality. Indeed, risk taking behaviours have been found to correlate with both benefits and costs in a wide range of taxa. For example, higher expression of activity (Lawler 1989; Azevedo-Ramos et al. 1992; Persons et al. 2001), boldness (Azevedo-Ramos et al. 1992; Dugatkin 1992; Biro et al. 2004) and aggression (Mehlman et al. 1994) have been found to correlate with increased mortality risk or proxies of mortality risk. In addition, activity (Laurila et al. 2008; Mas-Muñoz et al. 2011), boldness (Ward et al. 2004; Mas-Muñoz et al. 2011) and aggression (Turner and Iverson 1973) have been linked to benefits in terms of higher resource acquisition, or proxies of resource acquisition. Evidence for a risk-taking mediated trade-off between resource gain and survival has also been shown in killifish. Firstly, lab-based measurements of boldness in *Rivulus hartii* correlated positively to dispersal distance, growth rate and mortality (presumably due to predation) when fish had been released into natural conditions (Fraser et al. 2001). Second, it has been shown that aggression is associated with increased growth rates, and increased senescence in the killifish *Nothobranchius guentheri* (included in our study), which suggests a functional link between behaviour and life-history in this species (Markofsky and Perlmutter 1972, 1973; Haas 1976). Both *Rivulus hartii* (non-annual species) and *N. guentheri* (annual species) are also ecologically representative of other killifishes included in our study, both in terms of diet (mainly invertebrates), and habitat (sensu Furness 2016). Consequently, we predict that metabolism, and behaviours related to

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risk-taking and access to resources, should be positively associated with the pace of life-history.

METHODS

Study subjects

Twenty species of killifish (11 fast-living and 9 slow-living), suborder Aplocheiloidei, were included in this study. Eggs were sourced from dedicated hobbyists, or from our laboratory stock populations. The collection locale, and the time each species has been kept in aquaria since collection from the wild, is available in Table S1. Since resource demand and the trade-off between current and future reproduction are thought to drive the correlations between life-history and behaviour, we used reproductively active adult fish for all experiments. The species-specific means of life-history traits known to associate with a general pace of life (juvenile growth rate, time to maturity and reproductive rate), where taken from a parallel study (Sowersby et al. preprint). For further information on the study subjects, see the Supplementary Information.

Behavioural and physiological experiments

We measured behaviours previously linked to risk-taking and access to resources and mating opportunities, regarding activity, boldness and aggression (see Table 1 for a list of the measured variables and how we classified them). Additionally, we measured standard metabolic rate (SMR) as a proxy for daily energy expenditure (DEE), i.e. the energy allocated to both behaviour and life-history related physiological functions, such as egg and sperm production in the gonads (Daan et al. 1990). The behavioural experiments consisted of an open field test, an emergence test and a mirror test, conducted in that order for all individuals (for a list of the sample sizes in all experiments, see Table S2-S5). The median sample size

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per species for the behavioural (except aggression) and physiological tests was 14 individuals (range 4-31). Aggression was only measured in males, and consequently had a lower within-species sample size (median: 7 individuals, range: 2-11). Further information on the duration of the experiments can be found in the Supplementary Information. Individuals were tracked across experiments, with each individual measured once per experiment. However, we note that our unit of replication is species, and that each species is replicated by several individuals. Comparative models, across species, are contingent on the existence of biologically relevant species effects. We therefore also tested for species effects, calculated as the intraclass correlation (ICC) for species, for each of the traits that we measured (see below). Intraclass correlations range from 0 to 1, with higher values indicating that within species variation is low in comparison with among species variation (e.g. that members of the same species strongly resemble one another). We also used intraclass correlations to assess which measurements, nested under the behavioural trait categories that contained several traits (i.e. aggression and activity), best captured species effects of the particular trait category (using ICCest in the R-package ICC; Wolak et al. 2012).

Activity

We employed a standard open field test to estimate activity in a novel environment (as per Moran et al. 2017). Each fish was first placed gently into a transparent cylinder (10 cm diameter, as per Sowersby et al. 2015), within a larger cylindrical experimental arena (30 cm diameter, 10 cm water depth), with a camera mounted above. After a 5-minute acclimation, the transparent cylinder was carefully lifted, and the movements of the fish were recorded for 20 minutes. Raw data on movement and position of the fish was gathered using the software Ctrax (Branson et al. 2009). Measures of mean speed (cm/s), fraction of time spent moving, area explored and mean turning velocity (rad/cm swum) for each individual was obtained

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using the R package trackr ("https://github.com/Ax3man/trackr"). As the recorded variables where strongly correlated, where the dominant eigenvector explained 84% of the variation, only mean speed, based on its high intraclass correlation, was used in the models to ease interpretability of results. Note that all the traits are measured in the same trial, and therefore represent different estimates of how much an individual moves around in a standardized setting without threats. Mean speed should consequently not be interpreted as escape speed, where escape speed is generally expected to have a positive relation to survival in the presence of predators (Walker et al. 2005).

Boldness

Boldness-shyness was assessed using a test of latency to emerge into a novel environment (Burns 2008), measured in 59 x 29 cm opaque tanks, with a water depth of 10 cm, and bottom covered with fine white gravel. A shelter, (half terracotta pot, depth: 10 cm, width of opening: 10 cm, height of opening: 5 cm) was placed at one end of the tank, with a camera mounted above the entrance. Each fish was individually placed into the shelter and prevented from leaving by an opaque sliding door. After a 5-minute acclimation period, the door was removed, and the latency to emerge from the shelter into the novel environment was recorded (30 minutes), with individuals who took longer to leave the shelter being classified as shyer. The criterion for emergence was when more than half of the body (total length) was outside the shelter. A minority (9.3%) of individuals did not emerge and were assigned a maximum latency value of 30 minutes (see Irving and Brown 2013). A value of 1 was added to every value of latency to emerge (due to the presence of zeros in the dataset), after which it was log10-transformed to fulfil assumptions of normality. We then inverted and mean centred the axis by subtracting each value from the mean, so that larger values reflect bolder individuals.

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Aggression

To assess aggression levels, we exposed male killifish to a standard mirror test, which has previously been found to correlate with aggression towards conspecifics in fish (Earley et al. 2000; Wilson et al. 2011), including killifishes (Chang et al. 2012). Only males were tested, as male-male competition is typically the main driver of aggressive interactions in fish (Magurran and Garcia 2000). Mirror tests may overestimate scores for aggressive individuals, as all individuals will meet a size and condition-matched individual, aggression may escalate towards their mirror image more readily than to a live fish, thus inflating the variation of the measured trait (Arnott and Elwood 2009). However, as we were interested in correlations, rather than exact point estimates, and as positive reinforcement is unlikely to change the rank order of aggression among individuals (Johnsson and Näslund 2018), we view mirror tests as providing an appropriate measure of aggression at a comparative scale. Trial tanks were identical to housing tanks, and males were scored individually. The mirror (inserted after a 1-hour acclimation period) covered one entire, long side of the tank. Aggressive behaviour towards the mirror reflection was video recorded for 40 minutes. Using the software BORIS (Friard and Gamba 2016), we quantified three behaviours from the videos: number of tail whips, number of attacks and lunges, and the duration of display behaviour (i.e. lateral extension of gill lids, and/or posturing with fins extended). As the recorded variables where strongly correlated (a dominant eigenvector explained 62% of the variation), we chose to continue with the measure that best captured species effects (number of attacks - as determined by the largest intraclass correlation for species). We replaced 50% of the water between the trials of activity and boldness, and 100% of the water in between the aggression trials, to ensure consistently high-water quality.

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Standard Metabolic Rate

Metabolic rate was estimated from oxygen consumption over time using an intermittent-flow respirometry setup (Loligo® Systems, Viborg, Denmark), at 24 °C under a 12 hour day:night regime (07:00 - 19:00). Prior to testing, fish were fasted for 15 hours (8 hours in home tanks, 7 hours during acclimation period in measurement chambers) and weighed. Trials were run overnight, for approximately 17h. Oxygen consumption was measured in 30-minute cycles, during the period between 00.00 AM and 5:00 AM (when fish were likely to be least active), by estimating the slope of oxygen concentration decrease over time. Ten slopes were obtained for each individual over the measurement period, with only the mean value of the three minimum slopes, with $r^2 > 0.95$, then used to calculate mass specific SMR (i.e. divided by body weight) (Fry 1971; Schurmann and Steffensen 1997). We are confident that fish were resting during the measurement period, as the decrease in oxygen consumption over time was highly linear (typically $r^2 > 0.98$), implying fish were inactive. Background respiration (oxygen consumption by microorganisms) was assessed by conducting pre and post trial measurements and then subtracting the extrapolated value of background respiration from the total oxygen consumption at each moment in time, using the R package FishResp (Morozov et al. 2019). For a detailed version of the respirometry protocol see Supplementary Information.

Analysis of co-occurrence

We acknowledge the possibility that the ephemeral habitats inhabited by the fast-living species potentially contain fewer predatory fishes, than more stable habitats. Hence, risk-taking behaviours in these generally fast-living species could be under relaxed selection. To test this, we used an estimate of fish biodiversity for the habitat of each species, as a proxy for predation risk, collected from a database reporting co-occurring cyprinodontiform fishes

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(KilliData, www.killi-data.org), and assessed whether the number of co-occurring species was associated with the pace of life-history. We found that there was no significant effect of life-history on the number of co-occurring killifish species ($r = 0.381$, $df = 17$, $P = 0.108$).

Analysis of the potential effect of latitude on behaviour and metabolic rate

As species in our experiment come from a range of geographic latitudes (median range 10.8 N - 33.3 S), it is possible that differences in thermal optima might interfere with the expression of behaviours and metabolism. To test for potential biases due to optimal temperature differences, we correlated the absolute value of the latitude (absolute distance from the equator) at the collection point for each species (or when unavailable, the median latitude for all recorded collection points of the species) with the species means of our behavioural assays and metabolic rate test. None of these correlations were significant ($P > 0.26$ for all tests), indicating that different thermal adaptations are unlikely to explain our results.

Statistical analysis

Principal component analysis of life-history traits

We used a Probabilistic Principal Component Analysis (PPCA) on species mean values of log10-transformed time until sexual maturity in males (days), log10-transformed growth rate (cm/day), and reproductive rate (eggs/female/month), that were measured in Sowersby et al. (preprint), to obtain a proxy of the pace of life-history for each species (using the dominant eigenvector; see Auer et al. 2018). The total data set included life-history data for 12 additional species to increase the reliability of the PPCA, i.e. 32 species in total. Of the 60 possible values for the species included in this study (20 species times 3 variables), 6 were missing, and the PPCA was run with imputation of missing data (using the R package

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pcaMethods). The first principal component explained 75.4% of the variation in the data and was the only component that met the criteria of having an eigenvalue of 1 or higher to be included in further analyses (see Table S6).

Linear models

We were interested in the association between the continuous pace of life-history variable and the measured behavioural traits: activity, boldness and aggression, as well as metabolic rate. Using the R (R Core Team 2015) package MCMCglmm (Hadfield 2010), we fitted a multivariate model with our measures of activity, aggression, boldness and metabolic rate as response variables. Sex and life-history (estimated as species-specific PC1 scores), as well as their interaction, were added as fixed effects. The interaction was later dropped from the model, since the model could not converge with such a large number of parameters to estimate. Species identity, and a time-calibrated phylogeny (Furness et al. 2015) were included as random effects to account for non-independence of data points (Felsenstein 1985; Gelman and Hill 2007). All variance components, including the residual variance, were estimated separately for all response variables. By including life-history as a fixed effect in a regression model, we assume that life-history has a causal effect on the other traits. We did not test for the association between life-history and behavioural traits using correlations for two main reasons. Firstly, we had a clear prediction that the main driver of variation in life-histories is an environmental factor (pond desiccation), where fast-living annual species should have an increased need for resources, and a higher metabolic rate to convert these resources into energy. Since our hypothesized relationship is thought to be causal, a regression is to prefer over a correlation. Secondly, with smaller phylogenies it is difficult to partition (co)variances into components derived from common ancestry (phylogenetic effects) and species-specific effects (Housworth et al. 2004) - we could therefore not test

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these associations using correlations. While we did not have any primary interest in how these effects related to sex, we included sex in the model, as it has been proposed to mediate associations between life-histories and behavioural traits (Hämäläinen et al. 2018). For further information on residuals and priors, see the Supplementary Information.

Correlations among traits

In order to test for associations between the behavioural traits and metabolism, we used species level correlations (not phylogenetically controlled) rather than phylogenetically controlled regressions, since we had no *a priori* hypotheses regarding causation among the traits. We consequently tested for the presence of correlations among the behavioural axes and metabolism using a multivariate Bayesian mixed model. We used an intercept-only model with species as a random effect (estimating the full (co)variance matrix for species), and activity, boldness, aggression and metabolic rate as response variables. The species level correlations where subsequently calculated from the posterior distribution of the covariance. We initially attempted to partition among species variation into variance that is due to common ancestry (phylogenetic effects), and variance that is due to species-specific processes, in order to control for phylogenetic effects. However, in accordance with the low predicted statistical power of such partitioning of variance (Housworth et al. 2004), the error bars of the two components yielded inconclusive results, and thus we did not proceed further with such tests. Thus, the correlation estimates should be interpreted with caution, given that phylogenetic effects could not be controlled for.

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RESULTS

Linear models

The rather symmetric posterior distribution and the generally high estimates of the posterior mode of the intraclass correlations (ICCs), confirmed the presence of species effects in our measured traits (activity: $\log_{10}$-transformed mean speed, *ICC* = 0.545 (95% CI = 0.365, 0.755); boldness: log10-transformed and inverted latency to emerge +1, *ICC* = 0.447 (95% CI = 0.278, 0.651); aggression: number of attacks, *ICC* = 0.198 (95% CI = 0.0224, 0.464); and SMR: oxygen consumption rate, *ICC* = 0.257 (95% CI = 0.143, 0.509); see Table S7). Such effects are a prerequisite for finding among species effects of life-history.

When testing the effect of pace of life-history on the measured behavioural and physiological traits, we found that the pace of life-history was positively associated with aggression (number of attacks): estimate = 0.680 (95% CI = 0.133, 1.11), P_{MCMC} = 0.0240. However, we found no significant association between life-history and any of the other behavioural variables, or with physiology (measured as SMR) (activity: $\log_{10}$-transformed mean speed, estimate = 0.0165 (95% CI = -0.0779, 0.150), P_{MCMC} = 0.646; boldness: log10-transformed and inverted latency to emerge +1, estimate = 0.0132 (95% CI = -0.214, 0.263), P_{MCMC} = 0.854; and SMR: oxygen consumption rate, estimate = 1.37 (95% CI = -1.27, 3.55), P_{MCMC} = 0.342; see Tables S8 and S9, and Figure 1). In addition, we found no sex differences in any of the behavioural traits or SMR (activity: $\log_{10}$-transformed mean speed, P_{MCMC} = 0.512; boldness: log10-transformed and inverted latency to emerge +1, P_{MCMC} = 0.992; and SMR: oxygen consumption rate, P_{MCMC} = 0.158; see Table S8). We have included relevant summary statistics for each variable, subdivided by species, in the Supplementary Information (see Tables S11 to S14).

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Correlations among traits

We did not find any significant correlations among traits at the species level, i.e. all 95% credible intervals of the correlation estimates overlapped zero (metabolic rate - boldness = 0.478 (95% CI = -0.0205, 0.768); activity - boldness = 0.404 (95% CI = -0.0323, 0.744); activity - metabolic rate = 0.177 (95% CI = -0.211, 0.708); aggression - metabolic rate = 0.515 (95% CI = -0.108, 0.900); aggression - activity = -0.132- (95% CI = -0.539, 0.605); aggression - boldness = 0.276 (95% CI = -0.369, 0.745); see Table S10 and Figure 2).

DISCUSSION

Despite a clear theoretical prediction that risk-taking behaviours should coevolve with fast-slow life-history strategies (Biro and Stamps 2008; Réale et al. 2010; Dammhahn et al. 2018), this association has remained untested empirically on a comparative scale in a common-garden setting. Here, we tested the predicted covariation between life-history and risk-taking behaviours, measured in terms of activity, boldness and aggression, as well as standard metabolic rate, in a comparative, common-garden, multi-species system. We used multiple species of killifish, a system with extreme divergences in key life-history traits (Sowersby et al. preprint). We found significant variation across species for all measured traits, indicating that our behavioural assays were sensitive enough to identify species differences. Interestingly, of the traits we measured (activity boldness, aggression and metabolism) only aggression showed the predicted positive covariation with pace of life-history.

At the within species scale, different behavioural traits associated with risk-taking frequently cluster together along a proactive-reactive behavioural axis (Koolhaas et al. 1999; Groothuis and Carere 2005; Sih and Bell 2008), where proactive individuals are considered more risk-

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taking. However, until now, our knowledge regarding the evolutionary stability of this behavioural axis across species has remained limited (Sih et al. 2004a; Careau et al. 2009). Here, we found a non-significant trend that suggested a positive relationship between activity and boldness, potentially indicating that this expected association could be maintained at a macroevolutionary scale. Indeed, constraints on the independent evolution of behavioural traits, such as activity and boldness, might relate to common physiological regulation (Sih et al. 2004a), where similarities in the genetic regulation of neural and hormonal pathways restrict independent optimization of behaviour (Hämäläinen et al. 2018). Yet, due to the smaller size of our phylogeny, we did not manage to partition the estimated correlations into effects derived by common ancestry and species-specific processes, which could be an interesting avenue for future research.

While certain behavioural traits such as activity and boldness may covary at macroevolutionary timescales, we found that aggression showed only weak correlations with both activity and boldness. Interestingly, our results further indicate that aggression, rather than activity and boldness, correlated with life-history. Increased activity, boldness and aggression are known to incur costs, such as an increase in predation risk or injury, (Sih and Moore 1990; Skelly 1994; Anholt and Werner 1995; Laurila 2000; Biro et al. 2004), but also benefits, with more active, bold and aggressive individuals being more proficient in securing resources and mating opportunities (e.g. Fraser et al. 2001; Ward et al. 2004; Mas-Muñoz et al. 2011). In our study system, killifish males are aggressive, but do not generally defend territories (Berois et al. 2016). Furthermore, previous studies on *Nothobranchius guentheri* have shown limited female-choice (Polačik and Reichard 2009), which could indicate that access to mating opportunities is the main driver of male-male interactions (Polačik and Podrabsky 2015), where aggression may enable males to obtain higher reproductive success. Whereas, activity and boldness, may to a larger extent be more relevant for securing energetic

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resources rather than mating opportunities. In addition, we found no correlation between life-history and metabolic rate, indicating that differences in energy-use among species might not be tied to life-history strategy. This fact, and the fact that killifish species located at the faster end of the life-history continuum have some of the shortest life-spans recorded among vertebrates (Genade et al. 2005; Blažek et al. 2013; Berois et al. 2016), indicate that fast-living species might trade-off somatic maintenance for faster rates of growth and reproduction, instead of increasing resource acquisition through increased risk-taking. That is, if fast-living species and slow-living species have similar rates of energy acquisition, fast-living species may invest the energy gained into growth and reproduction to a larger extent than slow-living species (sensu Sowersby et al. preprint).

Risk-taking behaviour is assumed to be heavily influenced by evolution under different ecological conditions (Werner and Anholt 1993; Kolodny and Stern 2017), for instance, differences in predation levels could affect the balance between the costs and benefits of risk-taking behaviours. Differences in ecological conditions could therefore mask even the stark differences in life-histories present in our system, suggesting a more negligible role for pace of life-history in determining risk-taking across species. In our system, adaptations to ephemeral habitats likely played a major role in selecting for the fast life-history traits that we have observed in the so-called annual killifishes (see Sowersby et al. preprint). It is possible that inhabiting ephemeral ponds may have evolved as a predator avoidance strategy (Fraser et al. 2001). Yet, if fast-living species have evolved in environments with low levels of predation, compared to slow-living species, we would still expect fast-living species to employ more risk-taking behaviours, in order to maximize resource acquisition, with no constraints imposed by increased predation risk (Sih and Moore 1990; Skelly 1994; Anholt and Werner 1995; Laurila 2000; Biro et al. 2004). The putative presence of ecological differences between the fast-living and slow-living fishes should, if anything, reinforce the

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evolution of risk-taking, rather than obscure such differences. We used biodiversity as a proxy for the putative competitors and predators found co-occurring with the killifishes included in our study and did not find any relationship between the pace of life-history and species diversity. This suggests either that life-history, behaviour and metabolic rate evolve somewhat independently in killifishes, or that more subtle differences in ecological factors have strong effects on the functional role of behaviour. Here, the use of co-occurring species as a proxy for predation risk is based on an accessibility argument, specifically to test if the environments inhabited by fast-living species can be reached by species without specific adaptations to ephemeral habitats.

The results from our study should be interpreted with some caveats. Firstly, we assume that under natural conditions, the behavioural assays that we measured are relevant for resource acquisition, or for gaining mating opportunities, and simultaneously incur costs in the form of increased mortality risk. Previous studies have shown that killifishes exhibit the predicted patterns between the benefits and costs of risk-taking behaviours (Haas 1976; Fraser et al. 2001), and we have no reason to suspect that the species in our study differ with respect to the ecological settings of their habitats, in a manner that would make the risk-taking mediated trade-offs between resource acquisition and mortality different. Nonetheless, we cannot dismiss differences in ecological conditions as a potential explanation for the lack of association between life history and activity and boldness presented here. Secondly, another interesting possibility is that anti-predator behaviours are mainly plastic rather than innate, and that species clustered along the fast-slow axis of life-histories differ only in their potential for plastic responses to the presence of predators, where fast-living species would be less inclined to decrease their risk-taking behaviour in the presence of predators than slow species. This is a possibility that we cannot dismiss, as predatory avoidance in fish has previously been found to be highly plastic (Johansson and Andersson 2009). Finally, the

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species (not the individuals) that we included in our study have been under captive conditions for varying amounts of time. It is therefore possible that trait associations have eroded due to lack of selection or altered selection pressures under captive conditions (Vaz-Serrano et al. 2011). While we cannot dismiss this possibility, we note that the number of years since collection, and the life-history of the species included in this study do not covary (see Figure S1).

In addition, differential reproductive investment between the sexes has been suggested to underlie variation in behaviour (Bonduriansky et al. 2008; Hämäläinen et al. 2018). Yet, in congruence with the results of a recent meta-analysis (Tarka et al. 2018), we did not find any effects of sex on any of the examined traits. However, we note that the trait that we found to be correlated with life-history was aggression, a trait that is rather sex-specific in killifishes. In a parallel study, we found that species with faster life-histories tended to have larger and more exaggerated ornamental fins, than species with slower life-histories (Sowersby et al. in review). Moreover, the size of these ornamental fins correlated with decreased swimming abilities in males of fast-living species, while the females were less affected since their fins are smaller, which is predicted by theory (Andersson 1994). It is therefore possible that costly traits related to male mating success are predisposed to be affected by the trade-off between current and future reproduction, compared to female traits, but further studies are needed to confirm this.

In conclusion, when testing how risk-taking behaviour is associated with variation in the pace of life-history, we found that aggression coevolved with the pace of life-history, but not activity and boldness. Our results indicate that behaviours related to resource intake can evolve independently from life-history at a macroevolutionary scale, potentially due to energetic trade-offs involving other traits (such as somatic maintenance for instance). Taken

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together, our results further suggest that life-history variation may drive the evolution of behavioural differences among species, but at a trait specific level, and that subtle environmental differences might play an important role.

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FIGURES AND TABLES

Table 1. Categorisation of the behavioural and physiological traits that were measured.

Axes	**Traits**
Activity	Mean speed (cm/s) in the open field test
Boldness	Latency to emerge (s) from shelter in the emergence test
Aggression	Number of attacks directed at the mirror
Standard metabolic rate (SMR)	Oxygen consumption rate (mg O_2/kg/h) in metabolic rate test

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Figure 1. Points represent species means and error bars represent standard error of the mean. PC1 of life-history was obtained by extracting the first principal component of a PCA on log10-transformed time until sexual maturity in males (days), log10-transformed growth rate (cm/day), and reproductive rate (eggs/female/month). Activity is represented by log_{10}-transformed mean speed (cm/s), boldness is represented by log_{10}-transformed, mean centred and inverted latency to emerge +1 (s), metabolic rate is represented by log_{10}-transformed standard metabolic rate (mg O_2/kg/h), and aggression is represented by log_{10}-transformed number of attacks +1.

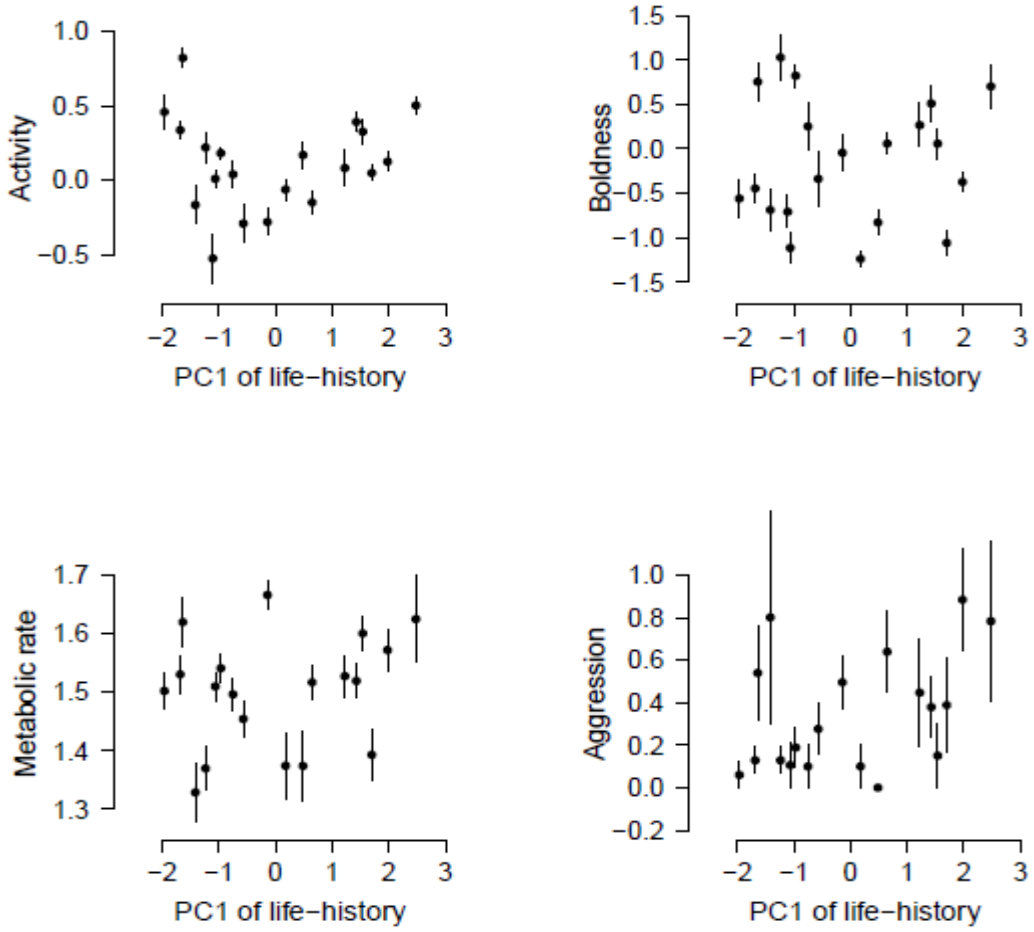

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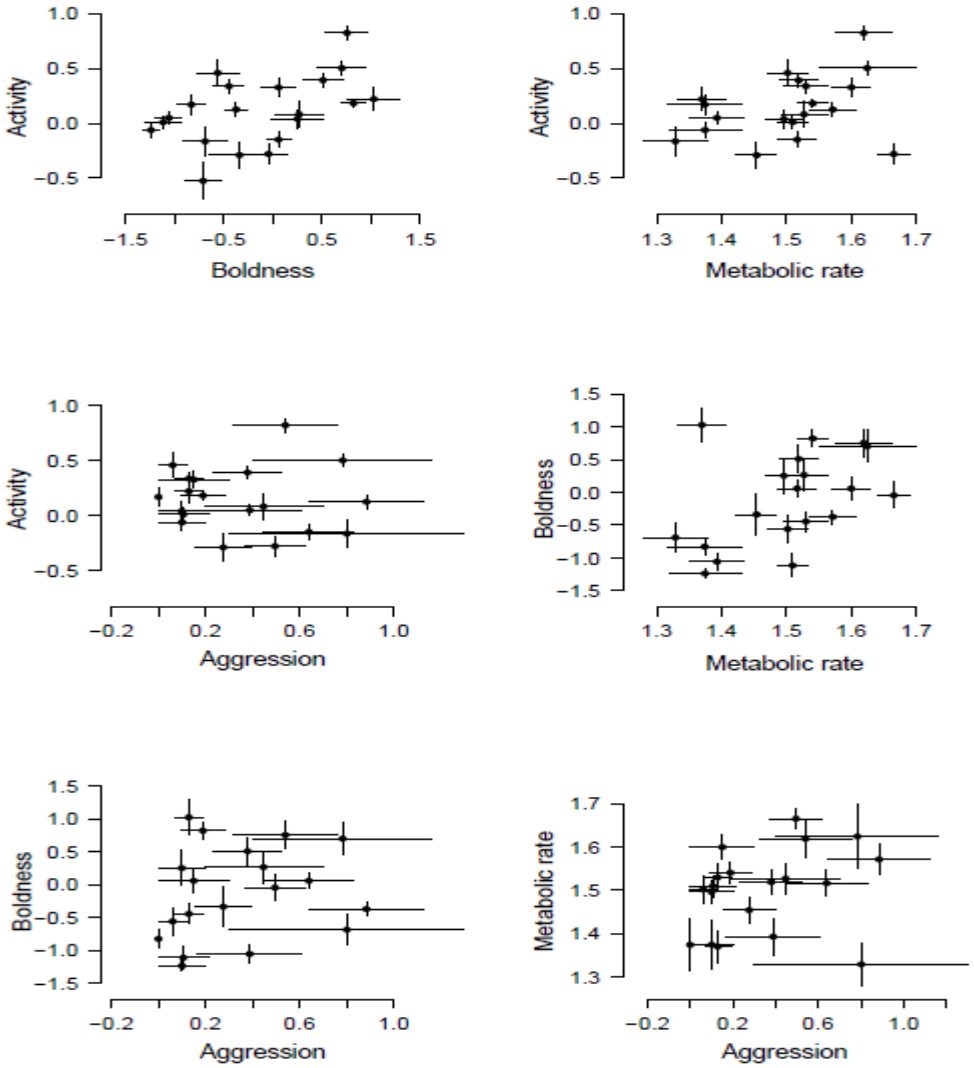
Figure 2. Pairwise scatterplots of all measured behaviours and metabolic rate. Points represent species means and error bars represent standard error of the mean. Activity is represented by $\log_{10}$-transformed mean speed (cm/s), boldness is represented by $\log_{10}$-transformed, mean centred and inverted latency to emerge +1 (s), metabolic rate is represented by $\log_{10}$-transformed standard metabolic rate (mg O_2/kg/h), and aggression is represented by $\log_{10}$-transformed number of attacks +1.



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